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NDVI-based productivity and heterogeneity as indicators of plant-species richness in boreal landscapes

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Decision making in managing biological diversity is critically dependent on adequate information concerning species-richness patterns and a rigorous understanding of species–habitat relationships. Measures of primary productivity derived from satellite images may provide useful cost-effective estimates of species richness and distribution patterns over wide areas. We constructed Generalized Additive models (GAM) to investigate the potential of primary productivity and its heterogeneity based on Normalized Difference Vegetation Index (NDVI) to explain the species richness in 28 separate vascular plant families in boreal forest landscapes, northern Finland. The productivity models explained on average more of the species richness than the heterogeneity models. However, models that performed best were produced by combining productivity and heterogeneity variables into the same models. Species richness responded mainly unimodally or positively to productivity and its heterogeneity. We conclude that measures of productivity and heterogeneity based on remote sensing can provide useful 'first filters' of locations of high diversity in plant families in boreal landscapes.

Introduction

Developing means for rapid forecasting of species richness and distributions using a few easily measured environmental variables is increasingly important in the assessment of impacts of anthropogenic and natural disturbances on biodiversity under limited resources (Kerr and Ostrovsky 2003, Seto *et al*. 2004). Remote sensing offers an inexpensive means to derive spatially complete environmental information for large areas in a consistent and regular manner (Muldavin *et al*. 2001, Foody and Cutler 2003). Such information may provide valuable tools for the prediction of spatial patterns of biodiversity attributes.

The current paradigm is that climate governs species distribution and richness patterns on broad biogeographical scales (Currie 1991, Huntley *et al*. 1995, Parmesan 1996, H-Acevedo and Currie 2003, Thuiller *et al*. 2004), whereas land cover and spatial distribution of suitable biotopes determine species occupancy patterns more than climate at finer spatial resolutions (Dunning *et al*. 1992, Opdam and Wascher 2004, Pearson *et al*. 2004, Thuiller *et al*. 2004). The

amount of energy available in a system, often measured as primary productivity, is also considered as one of the major determinants of biodiversity, especially species richness (Currie 1991, Rosenzweig 1995, Hawkins and Porter 2003). The Normalized Difference Vegetation Index (NDVI hereafter) (Tucker 1979) is one of the most extensively used remote-sensing based vegetation indices (for more discussion *see* Gould 2000, Nagendra 2001, Kerr and Ostrovsky 2003, Pettorelli *et al*. 2005). Remotely sensed NDVI observations provide direct estimates of primary productivity because NDVI measures the energy entering the ecosystem (Tucker and Sellers 1986, Reed *et al*. 1994, Paruelo *et al*. 1997, Mittelbach *et al*. 2001, Benayas and Scheiner 2002, Levin *et al*. 2007). Due to this intimate link between NDVI and primary productivity, NDVI has been found to be a useful predictor of regional variation in species richness (e.g. Gould 2000). NDVI is related to certain critical environmental factors (Seto *et al*. 2004), which improves its potentiality as a biodiversity predictor.

The relationship between primary productivity and species richness is generally assumed to be hump-shaped (Grime 1973, Rosenweig and Abramsky 1993, Waide *et al*. 1999, Mittelbach *et al*. 2001, Fairbanks and McGwire 2004), but other response shapes have also been observed (Mittelbach *et al*. 2001), including positive (Rosenweig and Abramsky 1993, Rosenweig 1995, Mittelbach *et al*. 2001, Whittaker and Heegaard 2003, Gillespie 2005) and negative ones (Oindo and Skidmore 2002). The position of the optimum productivity for species richness may be different for different species, ecosystems, observation scales and biogeographical regions (Waide *et al*. 1999).

Apart from the maximum or intermediate productivity, species richness also responds to variation in primary productivity (Rosenweig 1995, Kerr and Packer 1997, Hawkins and Porter 2003, Bailey *et al*. 2004). Heterogeneity in environmental factors is known to contribute to the diversity of plant communities (Ricklefs 1977, Grime 1979, Palmer 1994, Grace 1999, Lundholm and Larson 2003). Increase in heterogeneity implies an increase in niches, allowing more species to coexist. Spectral heterogeneity of remotely sensed images is related to the spatial heterogeneity of the environment, in particular to the plant species richness (Rocchini *et al*. 2004). For example, Gould (2000) showed that variation in NDVI can help in explaining the variation in species richness in arctic landscapes of Canada. The studies by Palmer *et al*. (2002), Rocchini *et al*. (2004), Rocchini *et al*. (2005) and Rocchini (2007) also revealed a significant relationship between heterogeneity and species richness, in their case from Mediterranean landscapes. The relationship between variation of NDVI in space and/or time ("heterogeneity in NDVI") and species richness has generally been found to be positive (Gould 2000, Oindo and Skidmore 2002, Fairbanks and McGwire 2004, Levin *et al*. 2007).

Several studies have highlighted the relevance of remote sensing information in biodiversity modeling (Gould 2000, Nagendra 2001, Kerr and Ostrovsky 2003, Pettorelli *et al*. 2005). However, there has been little effort to use such remote-sensing based estimators of habitat heterogeneity to predict species richness at the mesoscale, i.e. spatial resolutions ranging from 0.5 km to 2 km. Moreover, studies comparing predictions of species richness based on heterogeneity in NDVI with those based on NDVI primary-productivity values are largely lacking. In this study, we used mean and maximum NDVI values as a measure of primary productivity, and the range and standard deviation of NDVI values as a measure of the heterogeneity of productivity. The specific aims were to investigate the potential of (1) primary productivity and (2) heterogeneity to explain the richness patterns in 28 vascular plant families in a high-latitude forest landscape, northern Finland using plant species richness data from a spatial grid system (440 squares of 25 ha within an area of 110 km^2). We modeled the species richness in 28 plant families separately instead of using overall total species richness. This was because we were interested in investigating whether certain plant families are more closely related to NDVI-based predictors than others, and because different plant families may exhibit contradicting responses to productivity, making the overall richness–productivity relationships somewhat blurred.

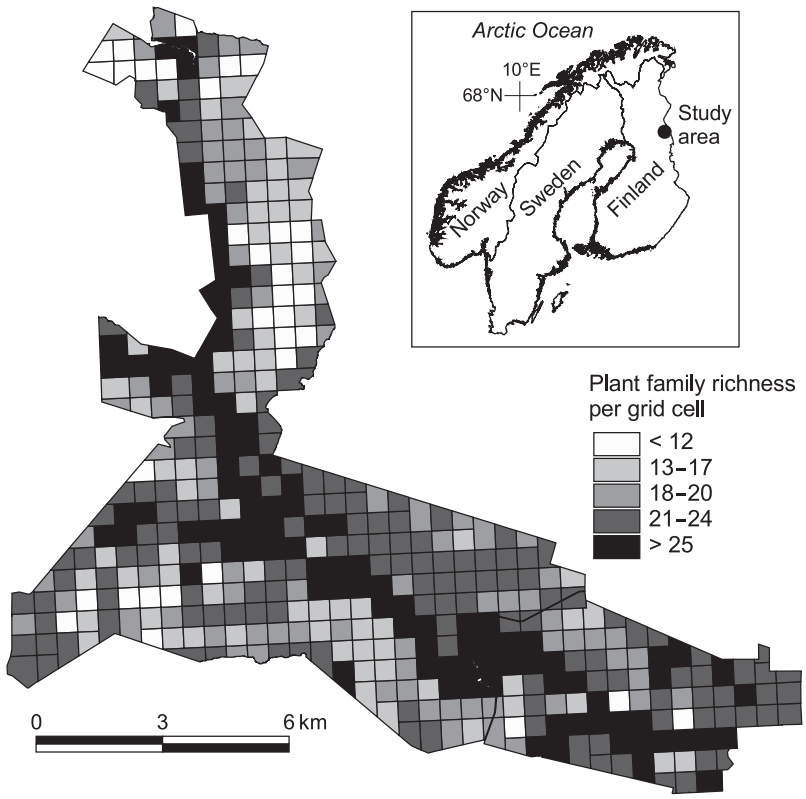

Fig. 1. A map of the richness of plant families in each of the 25-ha grid squares in the study area. The total number of families is 28.

Material and methods

Study area

The study area consists of 440 grid squares 25 ha in size and located in Oulanka National Park in northern Finland (66°22´N, 29°19´E) (Fig. 1). Oulanka National Park (total area = 27 746 ha) was founded in 1956. Oulanka National Park is located near the southern edge of the northern boreal-forest zone (Parviainen *et al*. 2008). The northern part of the study area is characterised by large open mires, whilst the southern part is dominated by forested hills, but also with mosaic of river valleys, water bodies, open bogs and mires. Dominant tree species are Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) and birches (*Betula* spp.). The vegetation is relatively rich with arctic, eastern, Siberian and southern species (Vasari *et al*. 1996). The mean annual temperature is ca. 0.5 °C, the growing season lasts ca. 128 days and the difference between the mean temperature of the coldest (January average ca. –14 °C) and the warmest (July average ca. 15 °C) month is ca. 29 °C (Atlas of Finland 1987). The climate in the region is thus more continental than in most other parts of northern Europe but with a maritime (humid) element added. Topography varies conspicuously and elevation ranges from 140 to 440 m a.s.l.

Plant family data

This study used the records of plant species found in the flora survey made by Söyrinki and Saari in the year 1980 (Söyrinki and Saari 1980). A total of 476 plant species were recorded in the survey. Plant data included detailed information on the geographical location of the occurrences (coordinates in the uniform grid system, Grid 27°E).

The data on the plant family richness (taxonomy follows Hämet-Ahti *et al*. 1986) for the 440 25-ha grid cells constituting the study area

were generated by calculating the number of species representing a certain plant family separately for each of the 28 plant families from the original georeferenced data of Söyrinki and Saari (1980). The plant family data for the study area consisted of richness records of 69 plant families. Of these families, 28 families with four or more records in the 440 grid squares of 25 ha and covering the whole study area were used in the analyses (Fig. 1 and Table 1). In total, 359 vascular plant species were included in the study. The most species-rich plant families were the Cyperaceae (58 species), Poaceae (47 species) and Asteraceae (22 species) (*see* Appendix 1 for a complete species list).

We are aware of the fact that there is a slight temporal mismatch between the plant species data (year 1980) and Landsat-imagery (year 2000). However, we assume that the effect of the temporal mismatch is only minor, since study area is a national park, where vegetation changes are relatively slow and human impacts very unsubstantial. Furthermore, the plant families found in the 1980s have principally been found also in later reinventories made in the same area.

Table 1. The total, minimum, mean and maximum numbers of species in the 28 vascular plant families, recorded from the 440 25-ha grid squares situated in Oulanka National Park, northern Finland.

Family	Total	Min	Mean	Max
Lycopodiaceae	5	0	1.9	4
Equisetaceae	8	0	4.1	8
Dryopteridaceae	13	0	1.7	8
Potamogetonaceae	9	0	0.6	5
Juncaceae	10	0	1.9	6
Poaceae	47	0	10.4	36
Cyperaceae	58	0	14.7	29
Orchidaceae	13	0	2.1	10
Salicaceae	16	0	5.2	10
Betulaceae	4	1	3.3	4
Polygonaceae	9	0	0.7	6
Caryophyllaceae	19	0	0.8	8
Ranunculaceae	14	0	2.8	10
Brassicaceae	12	0	0.5	8
Saxifragaceae	4	0	0.2	4
Rosaceae	16	0	6.8	13
Fabaceae	9	0	0.6	7
Violaceae	5	0	1.3	5
Onagraceae	6	0	1.5	5
Apiaceae	6	0	1.0	4
Pyrolaceae	6	0	2.6	6
Ericaceae	10	4	7.3	9
Rubiaceae	5	0	1.4	4
Lamiaceae	5	0	0.4	4
Scrophulariaceae	11	0	3.5	8
Lentibulariaceae	6	0	1.1	5
Asteraceae	22	0	3.4	13
Cichoriaceae	11	0	1.8	7
Total	359			

Remote sensing data

The Normalized Difference Vegetation Index (NDVI) (Rouse *et al*. 1973, Tucker 1979) is the most frequently used parameter for quantifying productivity and above-ground biomass of ecosystems (Tucker 1979, Box *et al*. 1989). It is based on the strong absorption of incident radiation by chlorophyll in the red (RED) spectral region, and the contrasting high reflectance by plant cells in the near infrared (NIR) region. Because NDVI is based on the normalized ratio of the reflectance in these two spectral regions (*see* the formula below), it is an indicator of the greenness of vegetation canopies, which enables separation of vegetation from other land coverage.

The NDVI was calculated for each 25-ha grid square using the formula:

$$NDVI = (NIR - RED)/(NIR + RED)$$

NDVI measures were generated from one geo-corrected Landsat ETM+ satellite scene (Table 2 and Fig. 2). The scene was acquired in July 2000 to coincide with the growing season. First, the Landsat scene was rectified according to digitized topographic maps (scale 1:20 000). The geometric correction of the planimetric root-mean-square error (RMSE) of test ground control points of the image was 7.9 m. The spatial resolution of the rectified Landsat TM image was set as 25 m, and new values for the pixels were resampled using a cubic convolution interpolation method (Hjort and Luoto 2006). Second, the image was topographically corrected using the 'Ekstrand correction method' (Ekstrand 1996). Finally, in order to decrease the effects of atmospheric variations, the image was atmospherically corrected using the SMAC algorithm, which is a semi-empirical correction method developed at the VTT, Technical Research Center of Finland

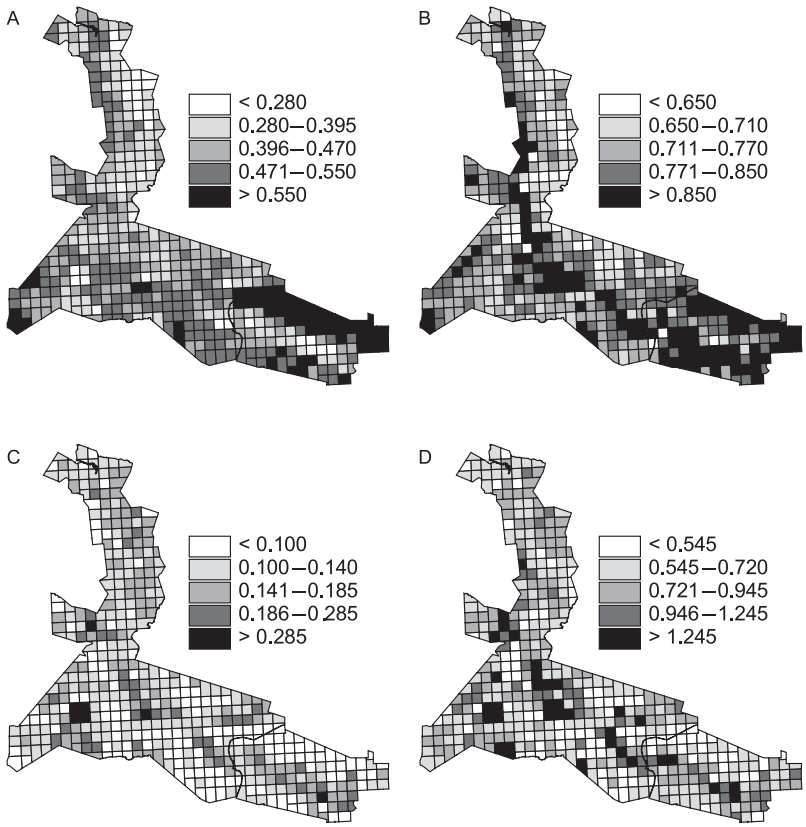

Fig. 2. Environmental variables calculated for each of the 25-ha grid squares: (**A**) mean NDVI, (**B**) maximum NDVI, (**C**) standard deviation of NDVI and (**D**) range of NDVI.

(Hjort and Luoto 2006). The satellite image was provided by the Finnish Environment Institute (SYKE) and orthorectified by METRIA, Sweden (Härmä *et al*. 2004).

Statistical analyses

GAMs

The 28 separate response variables, i.e. the number of species in each of the 28 vascular plant families, were related to the explanatory variables with generalized additive models (GAMs) (Hastie and Tibshirani 1990) using the GRASP ver. 3.2 package (Lehmann *et al*. 2002) for S-Plus ver. 6.1 (Insightful Corp., Seattle, WA, USA). GAMs are nonparametric extensions of generalized linear models (McCullagh and Nelder 1989). They have extensively been used in ecological applications (*see* Yee and Mitchell 1991, Guisan *et al*. 2002), because they permit both parametric and non-parametric additive response shapes, as well as a combination of the

Table 2. List of remote sensing variables (Landsat ETM+) used as explanatory variables in the modeling.

	Remote sensing variable	Abbreviation	Min	Max	Mean	SD
Productivity						
	Normalized Difference Vegetation Index (mean)	NDVI mean	0.067	0.656	0.442	0.101
	Normalized Difference Vegetation Index (max)	NDVI max	0.404	0.935	0.769	0.093
Heterogeneity						
	Normalized Difference Vegetation Index (SD)	NDVI SD	0.061	0.486	0.131	0.052
	Normalized Difference Vegetation Index (range)	NDVI range	0.354	1.723	0.752	0.275

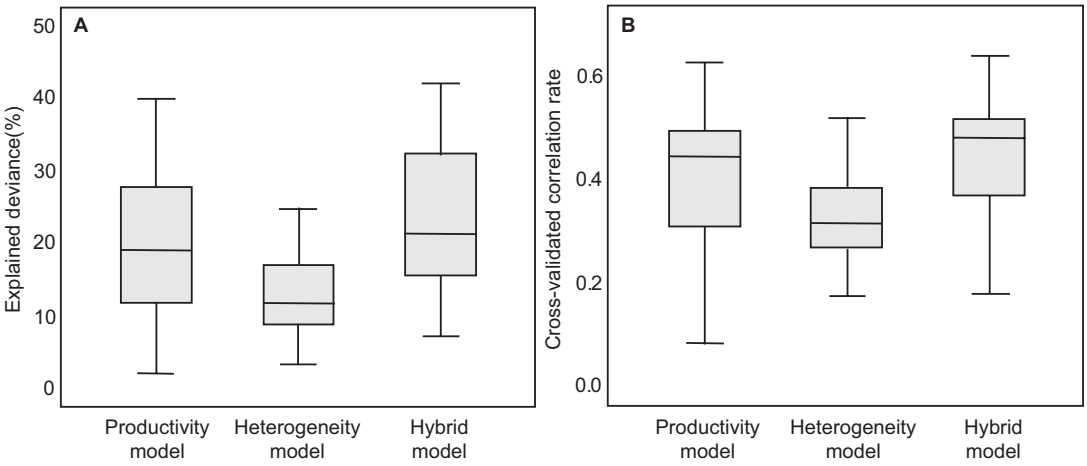

Fig. 3. (**A**) The amount of explained deviance (%) and (**B**) the cross-validated correlation values in the studied 28 plant families, derived from three different modeling settings. The boxes show medians, and 1st and 3rd quartiles values.

two within the same model (Wood and Augustin 2002). The GAM models were built using a stepwise selection procedure to select relevant explanatory variables, starting with a full model in which all predictors are fitted and alternately omitting and re-introducing one model component at each step. A Poisson probability distribution was selected for the response (count data), and the link function was set to logit. A smoothing spline method was chosen to smooth the studied variables, using 1 or 4 degrees of freedom (df) by default (Venables and Ripley 2002).

GAMs were fitted using three sets of explanatory variables for each of the 28 plant family richnesses. The first model for each family was built using mean and maximum values of NDVI in 25 ha grid squares; hereafter the productivity model. The second model was based on standard deviation and range in the NDVI values; hereafter the heterogeneity model. The final model (hybrid model) included all the productivity and heterogeneity variables.

The performance of models was evaluated using (1) the percentage of explained deviance (D^2), and (2) the correlation coefficient (r) between the observed and predicted values based on a four-fold cross-validation. The folds were generated by dividing the entire data set into four subsets, so that each subset contained an equal number of randomly selected data points. Each subset was dropped in turn from the data set, the model was calibrated with the three other subsets and the predictions were made for the omitted data points. After recombining the four folds, predictions were plotted against observed data (Lehmann *et al*. 2002).

Additionally, we validated visually the response curves to identify the correlation structure between response and remote sensing variables. Wilcoxon signed-rank tests were used to compare the performance of different competing models.

Results

The productivity models explained on average 19.5% of plant species richness and the heterogeneity models 12.9% (Fig. 3 and Appendix 2). The Wilcoxon signed-rank test revealed significant differences between these two models both in explained deviance (Wilcoxon signed rank test: $z = -3.652$, $p < 0.001$) and cross-validated correlation values ($z = -3.268$, $p = 0.001$) in favor of the productivity models. The productivity model explained best the richness of the Brassicaceae family (40.0%) and the heterogeneity model that of the Potamogetonaceae family (30.6%) (Appendix 2). Heterogeneity models for the families Equisetaceae (9.90%), Cyperaceae (8.95%) and Lentibulariaceae (7.51%) accounted for a higher amount of explained deviance than

the corresponding productivity models (7.09%, 2.72% and 1.97%, respectively), and the same also applied for cross-validated correlations (Appendix 2). Cross-validation correlation ratios of productivity and heterogeneity models were on average moderate, with mean r values of 0.40 with the productivity models and 0.32 with the heterogeneity models (Fig. 3 and Appendix 2).

Incorporating heterogeneity variables alongside productivity variables into the models improved the mean explanatory power (18.2%) and cross-validated correlation values (12.0%) statistically significantly (Wilcoxon signed rank test: $p < 0.001$) (Fig. 3 and Appendix 2). The highest improvement both in explained deviance and cross-validated correlation ratios was obtained with the families Cyperaceae (over 400% improvement in explained deviance and over 800% improvement in cross-validated correlation ratios compared to the productivity model) and Lentibulariaceae (over 300% and 200% improvements, respectively) (Appendix 2). Models for the families of Brassicaceae (42.1%), Lamiaceae (41.1%), and Potamogetonaceae (36.2%) gave on average the highest explained deviance ratios. The highest cross-validated correlations were obtained with the families Ranunculaceae ($r = 0.644$) and Lamiaceae ($r = 0.603$) (Appendix 2).

The range of NDVI values was the most frequently selected predictor of plant species richness. It was selected in 93% of the hybrid models (26 out of 28), whereas the mean and maximum values of NDVI both entered into 82.1% (23 out of 28) of the models (Table 3). A humped relationship between mean productivity (mean NDVI) and species richness was found in 60.9% of these cases (14 out of 23), followed by positive relationships (9 out of 23, 26.1%), as e.g. in the case of Orchidaceae (Fig. 4A) and Lycopodiaceae (Fig. 4B). In total, 20 models out of 23 (87.0%) found a positive relationship between maximum productivity measured as maximum NDVI and species richness, as compared with 2 hump-shaped (8.7%) and one negative (4.3%) relationships. The relationships between species richness and standard deviation in NDVI were mostly hump-shaped (8 out of 14, 57.1%). However, positive and hump-shaped relationships were equally common (12 out of 26, 46.2%) when heterogeneity was measured as range in NDVI values (Table 3). Species richness was associated negatively in 35.7% (5 out of 14) of the cases with standard deviation of NDVI, and in 7.7% (2 out of 26) of the cases with the range of NDVI. As an example, the shapes of the responses in univariate models for the families Orchidaceae and Lycopodiaceae are presented in Fig. 4.

In general, the highest Spearman rank correlations are between NDVI max and richness values, whereas the correlations between NDVI mean and richness values are typically rather low (*see* Table 4).

Table 3. Summary of the response shapes between the 28 plant species families and each remote sensing variable in the hybrid GAM models. For abbreviations of the remote sensing variables *see* Table 2. The direction of the effect is indicated with symbols (+ = positive linear correlate; – = negative linear correlate; ∩ = non-linear correlate with a hump-shaped response curve).

Family	NDVI			
	Mean	Max	SD	Range
Lycopodiaceae	+	+		
Equisetaceae	+			∩
Dryopteridaceae	+	+	–	+
Ranunculaceae	∩	+	∩	+
Betulaceae	∩			
Caryophyllaceae	∩	+	∩	+
Polygonaceae		+		∩
Violaceae	∩	+		+
Brassicaceae	∩	+		+
Salicaceae	∩		∩	∩
Ericaceae		∩		∩
Pyrolaceae	+	+	–	∩
Saxifragaceae	∩	+		∩
Rosaceae	∩	+	∩	∩
Fabaceae	∩	+	∩	+
Onagraceae	+		–	-
Apiaceae		+		+
Rubiaceae	∩	+	+	+
Lamiaceae	∩	+		+
Scrophulariaceae	∩	+		+
Lentibulariaceae		–		∩
Asteraceae	+	+		∩
Cichoriaceae	+	+	–	∩
Orchidaceae	+		–	–
Potamogetonaceae	∩	+	∩	+
Juncaceae		+		∩
Cyperaceae	∩	∩	∩	∩
Poaceae	+	+	∩	+
Count	23	23	14	26

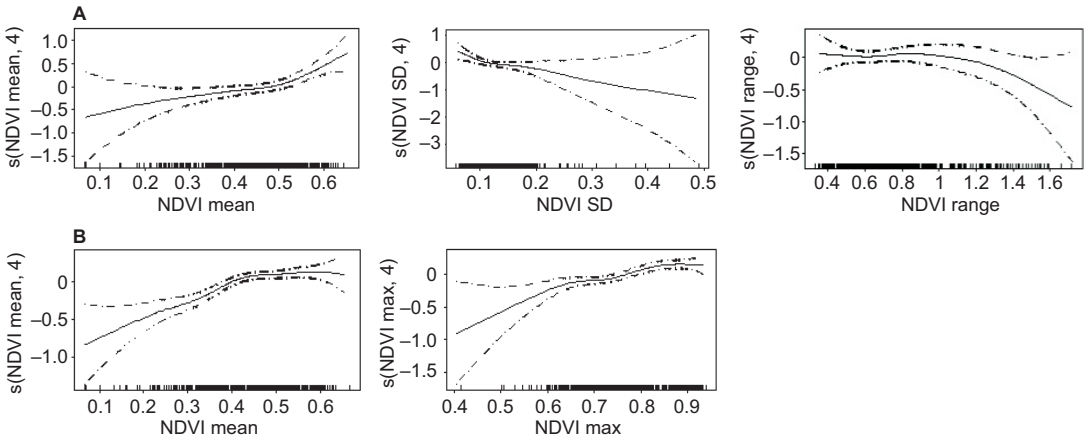

Fig. 4. Response shapes in the univariate GAM models for the families of (**A**) Orchidaceae and (**B**) Lycopodiaceae. The dashed lines are approximate 95% point-wise confidence intervals; tickmarks show the location of observations along the variable range; *y*-axis represents the effect of the respective variable; *s* represents the smooth term of GAM. For abbreviations of the environmental variables *see* Table 1.

Discussion

Vascular plant species richness is an important ecosystem feature and one attribute that characterizes the biodiversity of an area (Currie 1991, Gaston 2000, Gould 2000). The high-latitude environment restricts the presence and productivity of vascular plant species. In particular, low temperature, short growing season, low rates of soil nutrient cycling and extremes of soil moisture may limit primary productivity (Bonan and Shugart 1989). Therefore high-latitude landscapes are often considered to be relatively homogeneous in the structure of their vegetation and rather poor in species richness. However, such landscapes may comprise very different plant assemblages (Virtanen *et al*. 2006). For example, herb-rich forests within the boreal zone may be considerably rich in terms of their species diversity (Kuusipalo 1984, Heikkinen 1998), although they may cover only a fraction of the total forest area (Airaksinen and Karttunen 2001). Such areas are particularly important for the maintenance of biological diversity in boreal landscapes. Mesoscale biodiversity patterns are an important component of the diversity that occurs in a landscape or region, and represent also the scale at which management decisions are often made in terms of land use and conservation (Hill and Keddy 1992, Stoms 1994, Heikkinen 1998, Gould 2000).

Table 4. The Spearman rank correlation between NDVI based productivity and heterogeneity indices and richness of all plant species, herbaceous species, tree species and family richness (number of different plant families) in the studied 440 25-ha grids.

Richness	NDVI			
	Mean	Max	SD	Range
All plant species	0.125**	0.456***	0.188***	0.396***
Tree species	0.218***	0.413***	0.031^{NS}	0.252***
Herbaceous species	0.075^{NS}	0.417***	0.225***	0.414***
Family richness	0.159**	0.498***	0.167***	0.376***

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ^{NS} = non significant.

Explanatory power of the models

Our results suggest that NDVI provides a useful synthetic predictor that is significantly related to environmental variables affecting the richness of vascular plant species. Especially productivity measured as the mean and maximum NDVI values appears to account for a considerable amount of species richness within the different plant families. This is in agreement with earlier findings indicating that primary productivity is

one of the major determinants of species richness (Currie 1991, Rosenweig 1995, Hawkins and Porter 2003). The same authors have also showed that heterogeneity also often correlates positively with species richness. Heterogeneity of NDVI appears indeed to have a high predictive power for the species richness of a given site, across a range of spatial scales (Gould 2000, Kerr *et al*. 2001, Oindo and Skidmore 2002, Rocchini *et al*. 2004). Areas with a wide range of NDVI values, or with high standard deviations of the mean NDVI, are places where dense vegetation cover alternates with sparsely vegetated sites, or environments with different successional stages of vegetation — both of which may indicate high heterogeneity. However, in our study heterogeneity models explained on average less of the plant family species richness than the productivity models. This suggests that productivity is a stronger descriptor of mesoscale plant family richness patterns in high-latitude forest landscapes than heterogeneity (*see* also Levin *et al*. 2007). This result may be related to the scale-dependence of the relationship between heterogeneity and species richness (Palmer *et al*. 2002, Rocchini *et al*. 2004). As the size of sample plots increases, the importance of within-plot heterogeneity increases (Grace 1999). For example, Rahbek and Graves (2001) suggested that habitat heterogeneity may be a more significant determinant of larger scale diversity in some regions. However, our study area is located in boreal high latitude landscapes which are a relatively harsh environment for the species as compared with more southern temperate and tropical environments. A recent review by Hawkins *et al*. (2003) indicated that, at least on broad biogeographical spatial scales, energy- and productivity-related factors often play the most critical role in determining species richness of different organism groups especially in northern landscapes in Canada, Siberia and northern Europe. This is because available energy acts as the most critical limitation and thus constitutes the primary constraint for species richness in such environments.

However, incorporating heterogeneity variables alongside productivity variables improved the plant species richness models. Although the absolute increases in the amount of explained deviance and cross-validated correlations were generally small, they showed a clear trend and were statistically significant. Moreover, although the relative contribution of heterogeneity variables in our modeling experiment was rather low, they were selected into the majority of the models; 26 out of 28 models included at least one heterogeneity variable. Thus although productivity appears to be the prominent factor in explaining richness patterns, richness in most of the plant families can be increased due to increased habitat (productivity) heterogeneity. Physically and biologically more diverse environments enable finer-scale utilization of limited resources by different species in relatively small areas (Hawkins *et al*. 2003).

In summary, our results indicate that both productivity and heterogeneity play an important role in determining mesoscale species richness in high-latitude forest landscapes, because they reflect different aspects of productivity. In a similar vein, Foody and Cutler (2003) pointed out that more accurate information could be obtained using more complex approaches, e.g. by using standard deviation of NDVI alongside the mean values. The importance of productivity *vs*. heterogeneity appears to vary between plant families differing in their habitat requirements. For example, the explanatory capacity of the heterogeneity models was substantially higher that of the productivity models in the case of the families Equisetaceae, Potamogetonaceae and Lentibulariaceae. These families are known to prefer aquatic and shore habitats, where resource heterogeneity may be rather high.

The unexplained variation in our richness models was relatively high, which can be at least partly arise from unmeasured environmental variables (Austin 2002). In addition to productivity, other factors also affect species richness. One of these factors is topography (elevation, slope, aspect) (Austin 2002, Virtanen *et al*. 2006). Relationships between richness patterns and various ecological, geographical or other factors have been dealt in many papers (e.g. Currie 1991, Borcard *et al*. 1992, Heikkinen 1996, Iverson *et al*. 1997, Luoto 2000, Luoto *et al*. 2002, Wiens and Donoghue 2004). Thus, in detailed analyses of plant species richness in a landscape, several additional factors other than merely productivity should be taken into account.

Response shapes

Productivity measured as the mean NDVI values played a significant role in explaining species richness, showing mainly a hump-shaped species–energy relationship, where richness is reduced by abiotic stress at one end of the productivity gradient and by competition at the other (Grime 1979). Our findings are in line with those of former studies, in which a hump-shaped relationships between primary productivity and species richness have often been observed, especially at regional and smaller scales (*see* Currie and Paquin 1987, Wright *et al*. 1993 for more details, Rosenweig 1995, Grace 1999, Waide *et al*. 1999, Gaston 2000, Grime 2001, Mittelbach *et al*. 2001). Grace (1999) reviewed the literature on productivity–diversity relationships in herbaceous plant communities and concluded that most studies relating plant species richness to plant biomass in small plots showed a hump-shaped relationship. Mittelbach *et al*. (2001) also found that a unimodal relationship was detected most frequently when patterns were analyzed across vascular plant community types. At the individual species level, Waide *et al*. (1999) found that whereas hump-shaped relationships were common for some taxa and at some geographical and ecological scales, other patterns also occurred. Competition is probably the most reasonable explanation for a decline in species richness at high productivity levels, but other causes have also been proposed, including facilitation (Michalet *et al*. 2006), biogeographical affinity (Harrison and Grace 2007), differences in dispersal probability (Pärtel *et al*. 2007) and varying evolutionary processes (VanderMeulen *et al*. 2001, Bruun and Ejrnæs 2006). Furthermore, one potential explanation for hump-shaped patterns may be that spatial heterogeneity in resource availability is maximal at intermediate productivity, leading to the prevention of competitive exclusion between plant species (Tilman 1982). However, plant family richness was not always unimodally related with productivity. Many of the plant families, for example Dryopteridaceae, Orchidaceae, Ranunculaceae and Pyrolaceae, represented monotonically linear, positive association with the mean NDVI.

It should be noted that mean productivity reflects the average amount of biomass or resource variables, whereas maximum NDVI is more related to the highest potential productivity. In stable, highly productive habitats, competitively dominant species may monopolize space, excluding inferior competitors from the community. Biomass is high but species richness is low in such environments. Tropical rain forests are highly productive and have high biomass, they are relatively stable, and species richness is high. The majority of the plant family richness's examined in this study responded positively to high resource abundance indicated by high maximum NDVI values, suggesting that sites with potentially high productivity support more species than sites with lower potential. This is apparent as when the potentiality of productivity rises, the average variety of micronutrient combinations in fertile soils increases (Rosenweig and Abramsky 1993, Oindo and Skidmore 2002) leading to higher vegetative complexity (Bailey *et al*. 2004). The only negative response to maximum NDVI was obtained for the family Lentibulariaceae. This is ecologically reasonable, because the species of this family occur exclusively in shore habitats and shallow aquatic environments.

The shape of heterogeneity-richness relationships is generally positive (Gould 2000, Oindo and Skidmore 2002, Fairbanks and McGwire 2004, Levin *et al*. 2007). The variability of NDVI values usually reflects the heterogeneity of habitats, and is positively related with species richness of plants (Oindo and Skidmore 2002). However, in our study the responses between heterogeneity and species richness were mainly hump-shaped, indicating that the highest species richness occurs with moderate heterogeneity of productivity (Grime 1973, 1979). Our results showed that for example the family Salicaceae reaches its maximum species richness at intermediate levels of productivity and heterogeneity. The species of the Salicaceae family are well known to occur primarily in forests along riversides, and other places characterized by intermediate stages along the succession gradient in boreal forests. However, certain plant families in high latitudes appear to be specialized to the extremes of heterogeneity of primary productivity. For example the richness of the Orchidaceae family showed a clear nega-

tive relationship with heterogeneity. The species of the Orchidaceae family are rather demanding occurring strictly in stable old-growth forest, and a high level of heterogeneity may decrease habitat quality for them.

Conclusions

Developing conceptually simple models that are able to illustrate in a reliable manner how productivity and heterogeneity in productivity affect species richness may help the prediction of biodiversity in more remote and insufficiently surveyed areas. Such means can effectively decrease the need for extensive field sampling and can be essential for many conservation and management applications (Kerr and Ostrovsky 2003, Seto *et al*. 2004). Our approach, using continuous (unclassified) reflectance values provides a new possibility for researchers to develop relationships between species richness and remotely sensed data. Remotely sensed data allows trends over time to be examined, and areas of consistent high productive areas to be identified. Primary productivity and heterogeneity in the area, as estimated by using remotely sensed NDVI values, provide useful correlates of plant species richness in high-latitude areas. Spatial variability in species richness in 28 plant families was explained primarily by productivity, complemented by significant contributions from heterogeneity. Heterogeneity variables were often selected to species richness models at this scale and they showed mainly hump-shaped or linear responses.

These results have significant conservation implications. The role of both primary productivity and heterogeneity apparently was important in determining mesoscale species-richness patterns, more so than appears to be previously understood. Further work is needed to deepen our understanding of species density and to facilitate our ability to predict the responses of species richness to environmental changes. We conclude that remote-sensing based measures of productivity and heterogeneity have high potential as 'first filters' for identifying locations of high species richness in high-latitude forest landscapes.

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Appendix 1. A complete list of vascular plant species.

Species	Number of occupied cells
Lycopodiaceae	
Huperzia selago	107
Lycopodiella inundata	1
Lycopodium annotinum	382
Lycopodium clavatum	19
Diphasium complanatum	332
Equisetaceae	
Equisetum hyemale	113
Equisetum variegatum	76
Equisetum scirpoides	248
Equisetum fluviatile	298
Equisetum palustre	263
Equisetum sylvaticum	318
Equisetum pretense	297
Equisetum arvense	208
Dryopteridaceae	
Athyrium filix-femina	43
Diplazium sibricum	18
Cystopteris fragilis var. fragilis	42
Cystopteris fragilis var. dickieana	48
Cystopteris montana	90
Woodsia ilvensis	20
Woodsia alpina	46
Woodsia glabella	55
Matteuccia struthiopteris	37
Dryopteris carthusiana	11
Gymnocarpium dryopteris	335
Gymnocarpium continetale	40
Gymnocarpium robertianum	37
Ranunculaceae	
Trollius europaeus	251
Actaea erythrocarpa	155
Caltha palustris	191
Ranunculus repens	125
Ranunculus acris	160
Ranunculus monophyllus	10
Ranunculus auricomus	107
Ranunculus hyperboreus	2
Ranunculus lapponicus	2
Ranunculus reptans	104
Ranunculus peltatus	17
Ranunculus trichophyllus ssp. *trichophyllus*	2
Ranunculus trichophyllus ssp. *eradicatus*	10
Thalictrum flavum	102
Betulaceae	
Betula pendula	396
Betula pubescens	438
Betula nana	330
Alnus incana	350
Caryophyllaceae	
Arenaria ciliata ssp. *pseudofrigida*	13
Stellaria media	2
Stellaria graminea	63
Stellaria longifolia	9
Stellaria calycantha	45
Stellaria crassifolia	15
Cerastium alpinum	45
Cerastium fontanum ssp. *scandicum*	78
Cerastium fontanum ssp. *vulgare*	30
Sagina procumbens	3
Scleranthus annuus	1
Spergula arvensis	1
Lychnis alpina	1
Silene tatarica	10
Silene vulgaris	1
Silene latifolia ssp. *alba*	1
Silene dioica	1
Gypsophila fastigiata	15
Dianthus superbus	53
Polygonaceae	
Polygonum aviculare	1
Polygonum lapathifolium	1
Polygonum amphibium	5
Polygonum viviparum	246
Fallopia convolvulus	1
Rumex acetosella	32
Rumex acetosa	11
Rumex aquaticus	9
Rumex longifolius	5

continued

Appendix 1. Continued.

Species	Number of occupied cells
Violaceae	
Viola rupestris	70
Viola riviniana	8
Viola canina ssp. *montana*	154
Viola epipsila	313
Viola selkirkii	36
Brassicaceae	
Sisymbrium altissimum	1
Erysimum hieraciifolium	28
Erysimum cheiranthoides ssp. *cheiranthoides*	1
Erysimum cheiranthoides ssp. *altum*	1
Barbarea stricta	15
Rorippa palustris	10
Cardamine pratensis ssp. dentata	136
Draba norvegica	1
Draba cinerea	20
Capsella bursa-pastoris	2
Thlaspi arvense	1
Subularia aquatica	25
Salicaceae	
Salix pentandra	25
Salix reticulata	3
Salix myrsinites	186
Salix glauca	75
Salix phylicifolia	375
Salix myrisnifolia	152
Salix aurita	5
Salix caprea	408
Salix starkeana	22
Salix xerophila	8
Salix myrtilloides	204
Salix repens	1
Salix lapponum	292
Salix hastata	190
Salix pyrolifolia	1
Populus tremula	343
Ericaceae	
Calluna vulgaris	421
Rhododendron tomentosum	438
Arctostaphylos uva-ursi	130
Arctostaphylos alpina	2
Andromeda polifolia	322
Vaccinium oxycoccos	279
Vaccinium microcarpum	295
Vaccinium vitis-idaea	440
Vaccinium uliginosum	439
Vaccinium myrtillus	440
Pyrolaceae	
Pyrola minor	292
Pyrola media	12
Pyrola chlorantha	57
Pyrola rotundifolia	190
Orthilia secunda	365
Moneses uniflora	237
Saxifragaceae	
Saxifraga nivalis	68
Saxifraga hirculus	19
Saxifraga aizoides	9
Saxifraga cespitosa	6
Rosaceae	
Filipendula ulmaria	322
Rubus chamaemorus	351
Rubus arcticus	112
Rubus saxatilis	359
Rubus idaeus	145
Rosa majalis	141
Dryas oxtopetala	17
Geum rivale	299
Potentilla palustris	314
Potentilla nivea	13
Potentilla norvegica	2
Potentilla erecta	164
Fragaria vesca	75
Alchemilla glomerulans	1
Sorbus aaucuparia	377
Prunus padus	191
Fabaceae	
Astragalus frigidus	79
Astragalus alpinus	74
Oxytropis campestris	49
Vicia cracca	3
Vicia sylvativa	1
Trifolium repens	23
Trifolium hybridum	2
Trifolium pratense	11
Anthyllis vulneraria	3
Onagraceae	
Cincaea alpina	9
Epilobium angustifolium	360
Epilobium palustre	154
Epilobium davuricum	72
Epilobium hornemannii	29
Epilobium alsinifolium	16
Apiaceae	
Anthiriscus sylvestris	56
Cicuta vivosa	2
Carum carvi	2
Angelica sylvestris	245
Peucedanum palustre	19
Heracleum sphondylium ssp. *sibricum*	1

continued

Appendix 1. Continued.

Species	Number of occupied cells
Rubiaceae	
Galium boreale	168
Galium triflorum	2
Galium uliginosum	268
Galium palustre	184
Galium trifidum	14
Lamiaceae	
Scutellaria galericulata	100
Galeopsis speciosa	1
Galeopsis bifida	4
Prunella vulgaris	1
Thymus sepyllum ssp. *tanaënsis*	70
Scrophulariaceae	
Veronica serpyllifolia ssp. *serpyllifolia*	6
Veronica scutellata	17
Veronica longifolia	106
Melampyrum sylvaticum	309
Melampyrum pratense	430
Euphrasia frigida	140
Bartsia alpina	211
Pedicularis sceptrum-carolinum	50
Pedicularis palustris ssp. *borealis*	203
Rhinanthus minor	47
Rhinanthus serotinus	1
Lentibulariaceae	
Pinguicula alpina	132
Pinguicula villosa	34
Pinguicula vulgaris	118
Utricularia minor	28
Utricularia intermedia	125
Utricularia vulgaris	27
Asteraceae	
Solidago virgaurea	424
Erigeron acer ssp. *acer*	3
Erigeron acer ssp. *politus*	13
Erigeron acer ssp. *decoloratus*	34
Gnaphalium sylvaticum	7
Antennaria dioica	195
Inula salicina	10
Achillea ptarmica	2
Achillea millefolium	68
Tripleurospermum maritimum	3
Tripleurospermum inodorum	3
Matricaria matricarioides	2
Tanacetum vulgare	2
Artemisia vulgaris	1
Tussilago farfara	13
Petasites frigidus	83
Arnica angustifolia ssp. *alpina*	10
Senecio vernalis	1
Senecio vulgaris	1
Saussurea alpina	326
Cirsium helenioides	301
Cirsium palustre	1
Cichoriaceae	
Leontodon autumnalis	8
Sonchus asper	1
Lactuca sibirica	4
Cicerbita alpina	12
Taraxatum ssp.	189
Lapsana communis	1
Crepis paludosa	219
Crepis tectorum ssp. *tectorum*	3
Crepis tectorum ssp. *nigrescens*	2
Hieracium ssp.	349
Hieracium umbellatum	45
Orchidaceae	
Cypripedium calceolus	59
Epipactis atrorubens	30
Epipogium aphyllum	4
Listera ovata	13
Listera cordata	118
Goodyera repens	75
Corallorhiza trifida	52
Calypso bulbosa	56
Coeloglossum viride	126
Gymnadenia conopsea	162
Dactylorhiza incarnate	41
Dactylorhiza traunsteineri	35
Dactylorhiza maculata	193
Potamogetonaceae	
Potamogeton filiformis	8
Potamogeton compressus	1
Potamogeton berchtoldii	19
Potamogeton alpinus	87
Potamogeton natans	31
Potamogeton gramineus	84
Potamogeton lucens	2
Potamogeton praelongus	2
Potamogeton perfoliatus	46
Juncaceae	
Juncus bufonius	2
Juncus alpinus ssp. *nodulosus*	43
Juncus filiformis	105
Juncus stygius	111
Juncus triglumis	28
Luzala pilosa	412
Luzula multiflora ssp. *multiflora*	3
Luzula multiflora ssp. *frigida*	36
Luzula sudentica	66
Luzula pallescens	31

continued

Appendix 1. Continued.

Species	Number of occupied cells	Species	Number of occupied cells
Cyperaceae		*Carex serotina* ssp. *pulchella*	1
Eriophorum vaginatum	320	*Carex lasiocarpa*	274
Eriophorum brachyantherum	25	*Carex vesicaria*	103
Eriophorum russeolum	3	*Carex rotundata*	2
Eriophorum scheuchzeri	3	*Carex rostrata*	325
Eriophorum angustifolium	260		
Eriophorum latifolium	182	**Poaceae**	
Eriophorum gracile	13	*Molinia caerulea*	334
Schoenoplectus lacustris	14	*Phragmites australis*	119
Trichophorum alpinum	249	*Nardus stricta*	2
Trichophorum cespitosum	259	*Melica nutans*	310
Eleocharis palustris ssp. *palustris*	1	*Festuca ovina*	278
Eleocharis acicularis	10	*Festuca rubra*	143
Eleocharis quinqueflora	23	*Festuca pratensis*	2
Schoenus ferrugineus	9	*Lolium perenne*	2
Rhynchospora alba	1	*Lolium multiflorum*	1
Carex capitata	92	*Poa annua*	13
Carex pauciflora	195	*Poa trivialis*	12
Carex chordorrhiza	248	*Poa alpina*	38
Carex dioica	282	*Poa pratensis*	1
Carex heleonastes	18	*Poa subcaerulea*	3
Carex canescens	283	*Poa alpigena*	211
Carex brunnescens	109	*Poa nemoralis*	145
Carex disperma	2	*Poa glauca*	9
Carex tenuiflora	10	*Poa palustris*	5
Carex loliacea	131	*Dactylis glomerata*	1
Carex elongata	1	*Deschampsia cespitosa*	268
Carex echinata	15	*Deschampsia flexuosa*	437
Carex diandra	46	*Calamagrostis epigejos*	210
Carex appropinquata	15	*Calamagrostis canescens*	5
Carex aquatilis	28	*Calamagrostis purpurea* ssp. *phragmitoides*	364
Carex acuta	109	*Calamagrostis stricta*	49
Carex nigra ssp. *nigra*	4	*Calamagrostis lapponica*	309
Carex nigra ssp. *juncella*	295	*Agrostis stolonifera*	29
Carex cespitosa	244	*Agrostis gigantea*	8
Carex elata ssp. *omskiana*	1	*Agrostis capillaris*	134
Carex buxbaumii ssp. *buxbaumii*	128	*Agrostis canina*	3
Carex buxbaumii ssp. *mutica*	7	*Agrostis mertensii*	193
Carex norvegica ssp. *inferalpina*	112	*Alopecurus pratensis*	4
Carex vaginata	259	*Alopecurus arundinaceus*	1
Carex panicea	91	*Alopecurus geniculatus*	1
Carex livida	82	*Alopecurus aequalis*	20
Carex magellanica ssp. *irrigua*	288	*Phleum pratense*	8
Carex limosa	223	*Phleum alpinum*	136
Carex rariflora	1	*Phalaris arundinacea*	187
Carex laxa	17	*Hierochloë hirta* ssp. *arctica*	68
Carex globularis	389	*Anthoxanthum odoratum*	136
Carex ericetorum	45	*Milium effusum*	104
Carex digitata	76	*Bromus hordeaceus*	2
Carex glacialis	10	*Elymus repens*	1
Carex capillaris	165	*Elymus caninus*	195
Carex flava	228	*Elymus fibrosus*	8
Carex jemtlandica	14	*Elymys alaskanus*	45
Carex bergrothii	27	*Hordeum jubatum*	1

Appendix 2. Explained deviance and cross-validated (cvCOR) values of the productivity, heterogeneity and hybrid (productivity + heterogeneity) model. cvCOR values were calculated as the Pearson correlation index between the observed and predicted values of species richness.

Family	Productivity model		Heterogeneity model		Hybrid model	
	Explained deviance (%)	cvCOR	Explained deviance (%)	cvCOR	Explained deviance (%)	cvCOR
Lycopodiaceae	12.824	0.372	3.756	0.177	12.824	0.372
Equisetaceae	7.086	0.254	9.886	0.298	13.346	0.366
Dryopteridaceae	29.012	0.505	11.860	0.307	31.367	0.502
Ranunculaceae	37.715	0.632	18.962	0.439	39.993	0.644
Betulaceae	9.663	0.278			9.663	0.278
Caryophyllaceae	33.142	0.525	17.896	0.347	35.656	0.536
Polygonaceae	15.657	0.334	8.735	0.284	16.706	0.398
Violaceae	19.064	0.484	14.267	0.401	20.869	0.506
Brassicaceae	39.970	0.552	24.749	0.404	42.128	0.576
Salicaceae	10.656	0.294	8.725	0.255	16.804	0.337
Ericaceae	7.567	0.268	7.416	0.206	15.532	0.373
Pyrolaceae	17.855	0.453	7.923	0.272	18.643	0.45
Saxifragaceae	20.253	0.322	12.853	0.26	23.592	0.382
Rosaceae	21.006	0.462	12.527	0.34	24.992	0.491
Fabaceae	32.348	0.527	16.331	0.304	34.516	0.548
Onagraceae	18.186	0.431	10.213	0.313	20.808	0.463
Apiaceae	12.960	0.404	8.748	0.347	15.303	0.447
Rubiaceae	16.366	0.452	11.778	0.374	20.814	0.484
Lamiaceae	38.126	0.586	23.784	0.444	41.050	0.603
Scrophulariaceae	21.014	0.46	18.015	0.421	25.185	0.504
Lentibulariaceae	1.970	0.0853	7.512	0.209	8.007	0.264
Asteraceae	23.842	0.487	10.049	0.299	24.912	0.494
Cichoriaceae	23.689	0.492	9.656	0.336	25.068	0.507
Orchidaceae	5.521	0.18	3.151	0.0261	7.142	0.18
Potamogetonaceae	26.517	0.471	30.635	0.524	36.159	0.569
Juncaceae	10.708	0.305	12.119	0.318	15.436	0.372
Cyperaceae	2.716	0.0326	8.952	0.269	14.020	0.316
Poaceae	29.346	0.539	18.625	0.419	33.553	0.57
Mean	19.456	0.400	12.930	0.318	23.003	0.448
SD	10.847	0.147	6.433	0.099	10.291	0.112